Introduction, Phenology, and Density of Yellow Starthistle in Coastal, Intercoastal, and Central Valley Situations in California

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ABSTRACT

Yellow starthistle, *Centaurea solstitialis* L., is believed to have originated is Eurasia. More than 1.9 million acres are infested in California where it colonizes rapidly on disturbed soils. It is allelopathic and forms dense stands. When ingested by horses, yellow starthistle causes "chewing disease." Its chronology of introduction in California has been associated with the brick floras in the Mexican or postmission period after 1824. Its field phenology consists of 9 primary growth stages (= phenophases) and 17 substages. A description and key are provided.

The coastal population had a greater average population density, average plant height, and earlier phenology than did the intercoastal and valley populations. Differences in average precipitation and temperature, seed production, and ratio of kinds of seeds produced were noted at the compared sites. Evidence suggests that California plants are represented by different allopatric populations responding by genotypic differentiation to environmental differences in their habitats. This study is the necessary basis for the biological control investigations of this weed.

KEYWORDS: Yellow starthistle; yellow starthistle phenology, growth of yellow starthistle; yellow starthistle in California.

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INTRODUCTION, PHENOLOGY, AND DENSITY OF YELLOW STARTHISTLE IN COASTAL, INTERCOASTAL, AND CENTRAL VALLEY SITUATIONS IN CALIFORNIA

By D. M. Maddox[1]

INTRODUCTION

Yellow starthistle, *Centaurea solstitialis* L., is of great economic importance in California where it has invaded grainfields, orchards and vineyards, other cultivated crops, pastures and rangelands, and roadsides and wastelands. It has been ranked seventh in importance out of the 29 worst weeds in California. In 1965, an estimated 1.9 million net acres were infested in California (Koehler *1965*).[2] The present infested acreage is not known, although it is conceded to have increased sizeably.

This species is potentially menacing to rangelands because of its ability to spread rapidly and colonize on disturbed soils. It forms dense infestations, and like many other *Centaurea* species, it exhibits an allelopathic effect on associated species, therefore reducing the available edible forage. Robbins et al. (*1951*) commented that it is a contaminant in commercial seeds and hay and listed it as an important weed of alfalfa and cereal grains.

Ingestion of the plant by horses produces a nervous syndrome called "chewing disease," which results in brain lesions and mycosal ulcers in the mouth, and can eventually culminate in death (Kingsbury *1964*). The disease has only been reported in horses; comparable symptoms have not been seen in other animals. A more thorough discussion can be found in the papers of Cordy (*1954a*, *1954b*) and Mettler and Stern (*1963*).

In 1969, a seed fly, *Urophora sirunaseva* (Hering), was introduced in California for the biological control of *Centaurea solstitialis* L. by the University of California. Although the fly was found to be host specific on C. *solstitialis* in Italy, it failed to develop and establish on the California plants. Because of this apparent anomaly, I selected three climatically different habitats as a preliminary effort towards understanding the California plant types. I first examined these plant types and tried to determine their probable geographic

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[2]The year in italic, when it follows the author's name, refers to Literature Cited, p. 13.

origin, thus enhancing the possibility of finding natural enemies that had evolved from similar plant types. Furthermore, since no information was available concerning the plant's periodic biological events, I had to study the phenology in the different habitats to facilitate a comparison. This study was necessary to provide certain baseline information for the biological control investigation of yellow starthistle.

DESCRIPTION, GEOGRAPHIC DISTRIBUTION, AND DIVERSITY

Description

Yellow starthistle is an annual herb that occasionally exhibits a biennial habit. The mature plants are 3 to 7 decimeters tall and possess a vigorous taproot. The stems are erect, stiff, winged, and branched. The basal leaves are rosulate and pinnatifid with large terminal lobes. The cauline leaves are sessile, decurrent, linear-lanceolate, alternate, and cottony pubescent. The flowers are yellow and develop into two types of achenes, light colored with pappus and dark without pappus. The plant is characterized by the involucral bracts having a stiff, terete, yellow, divergent spine, 1 to 2 cm long, with one or more pairs of short, lateral spines at its base (Munz and Keck *1959*, Roche *1965*).

Geographic Distribution

The center of geographic distribution of yellow starthistle is believed to be Eurasia. Komarov (*1934*) listed this species in Iran, Armenia, Kurdistan, Balkan-Asia Minor, Mediterranean region, southcentral Europe, and as an adventive in Atlantic Europe and North America. Although most authors consider it to be endemic to the Mediterranean, Prodan (*1930*) believes it invaded that area from the Orient. In North America, the species has become colonized in Washington, Oregon, Idaho, and California and was scattered throughout much of the United States and north into Canada from Ontario to British Columbia (Reed and Hughes *1970*). In California, it is found primarily throughout the Sacramento Valley, the north Coastal Range, the San Francisco Bay region, and south into the San Joaquin Valley (Robbins et al. *1951*).

Diversity

There are no records of hybridization of yellow starthistle with other *Centaurea* species, although many *Centaurea* species do hybridize readily (Marsden-Jones and Turrill *1954*, Stace *1975*). Evidence supporting ecotypic variation in this species is apparent; however, and T. C. Fuller (personal communication) has commented that the California introductions quite possibly represent a relatively small part of the gene pool of the species. Roche's (*1965*) studies have also demonstrated that this species exhibits a great amount of genetic plasticity, as indicated in the significantly different variations in phenology and morphology recorded among his source materials. Furthermore, R. G. Emge's (unpublished data) preliminary studies with exotic *Puccinia* rust fungi, col-

lected from Turkey, have shown that only some *C. solstitialis* plants from different localities in California are susceptible to infection when tested with these rusts.

Puccinia species are usually very specific, and in many cases even race specific. In addition, previous studies (D. M. Maddox and N. A. Stevens, unpublished data) also show that the phenology of yellow starthistle populations at Hopland is different from that of populations growing at Woodland and Concord, Calif., when grown under standard conditions. Such evidence suggests that more than one type is currently present in California.

HISTORICAL ORIGIN IN CALIFORNIA

The studies of Hendry (*1931*) and Hendry and Bellue (*1936*) provide some insight into the approximate chronology of introduction of yellow starthistle in California. Although Parish (*1920*) had stated that no alien weed species had penetrated Alta California prior to colonization in 1769, this was challenged by the data presented by Hendry (*1931*). Hendry found seeds of the alien weeds *Rumex crispus* L., *Erodium circutarium* H'Her., and *Sonchus asper* L. in the oldest walls of several mission buildings established in the premission period before 1769. An analysis of adobe bricks from buildings of both the Spanish and Mexican periods by Hendry (*1931*) and by Hendry and Bellue (*1936*), to determine the early occurrence of both native and alien plant species in California, showed that yellow starthistle was not present in the brick floras of the Spanish period from 1769 to 1824 but was present in the Mexican or postmission period after 1824.

Furthermore, my studies of early California collections deposited in the herbaria of the California Academy of Sciences and the University of California at Berkeley and Davis, showed that the earliest specimen collected was in 1869 at Oakland, Calif., and the next earliest was in 1887 at Vacaville, Solano County, Calif. Subsequent to these dates, numerous collections were made throughout northern California in the 1890's and continued to increase in number during the 1900's.

MATERIALS AND METHODS

Yellow starthistle populations were studied in three California areas because they provided different climatic conditions of temperature and precipitation. The locations and habitats selected were Hopland (coastal), Concord (intercoastal), and Woodland (valley). Studies were carried out during 1976, 1977, and 1978. Distinct growth stages (= phenophases) were necessary for recognition. The generally accepted phenophase terminology, such as cotyledon and rosette, was applied to primary phenophases; however, the substages, such as la through 3b, early rosette phase, late rosette phase, initial bolt phase, and early bolt phase, were based on an arbitrary selection.

A rectangular plot, measuring 22 by 12 m, was established at each location using permanently marked stakes placed every 2 m around the entire perimeter.

A total of 50 points was established within the plot (each point 2 m equidistant from its nearest neighbor), using 12.7-cm nails marked with orange survey tape for permanent marking. Yellow starthistle densities were determined using a modified "point-centered quarter" method, such as that used by Dix (*1961*). The area around each point was divided into quarters using a wire crossbar, and within each quarter the closest living yellow starthistle plant to the point was examined. The following data were recorded: stage of plant development, distance of the plant from the point, plant height, and plant width. From these data, the average distance between plants, average area in square centimeters per plant, and total density of plants per sqaure meter were calculated using the methods of Dix (*1961*). The number and percentage of the yellow starthistle growth stages present at the time of data acquisition were also determined. Data were taken on a monthly basis, and observations were made intermittently.

Soil moisture was determined at all three sites during 1976 for March through September. Standard 5- by 7.5-cm aluminum soil cans were used to collect soil samples at a 15-cm depth. The difference between fresh and dry weights was determined after allowance had been made for the container, and the percentage of soil moisture in the sample was calculated and recorded.

The germination of seeds in the soil reservoir was carried out as a one-time study for February through May 1977 at all sites. This period was chosen because yellow starthistle seed germination is correlated with the winter-spring rain cycle in California. A series of five 30-cm^2 areas was established around the perimeter of each site, and the seedlings that germinated were counted and removed monthly.

Other data recorded by either measurement, dissection, or counting included the following: average height and width of mature plants, average number of seed heads per plant, average number of seeds per seed head, average number of pappus-bearing seeds per head, average number of nonpappus-bearing seeds per head, and average number of seeds per plant.

Weather records at the Hopland site were supplied by the Hopland Field Station of the University of California, since their recording station was comparable to the site as regards elevation (valley floor condition) and was approximately 3 km from the study site. At the Concord site, precipitation measurements were supplied by the Office of Emergency Services, Contra Costa County (1.5 km from site), and temperature data were supplied by the National Weather Service at Buchanan Field Airport located adjacent to the site. Weather records for the Woodland site were also supplied by the National Weather Service reporting station in Woodland.

RESULTS

Phenophases: Number, Description, and Identification

Number of Phenophases

Yellow starthistle undergoes a total of 9 primary growth stages (= phenophases), some of which can be further divided into 17 recognizable substages.

These stages are as follows:

I. Seedling stage (6 substages)
II. Rosette stage (2 substages)
  Early rosette phase
  Late rosette phase

III. Vegetative stage (bolting) (3 substages)
  Initial bolt phase
  Early bolt phase
  Late bolt phase

IV. Floral bud stage (bud formation) (4 substages)
V. Anthesis (flowering) (2 substages)
VI. Seed formation stage
VII. Mature stage
VIII. Seed dissemination stage
IX. Senescence stage

Description of Phenophases

Cotyledon stage 1a.--This stage possesses only two seed leaves. The green leaves are oblong and tongue shaped. The average height is about 0.9 cm, and the average spread of the seed leaves is about 1.5 cm (table 1).[3] The roots lack pigmentation, and the stem is usually opaque and may be faintly red (fig. 1).[4]

Seedling stage 1b.--These seedlings have three or four leaves and one or two secondary leaves in addition to the seed leaves. The secondary leaves are longer and narrower. The average height is about 1.1 cm, and the average spread of the leaves is about 1.6 cm (table 1). The stem is opaque, usually faintly red. The three-leaf form is shown in figure 2 and the four-leaf form in figure 3.

Seedling stage 2a.--These plants are characterized by having five to eight basal leaves. All but two are secondary leaves, and all are entire (fig. 4). Their average height is 1.3 cm with an average leaf spread of about 3.0 cm (table 1). The roots usually contain some reddish pigmentation.

Seedling stage 2b.--This stage also has five to eight basal leaves. One or two of these leaves are only partly lobed at the base (fig. 5). These plants average about 5.6 cm in height with an average leaf spread of about 5.8 cm (table 1). A reddish pigmentation is usually present in the roots.

Seedling stage 3a.--This stage is characterized by five to eight basal leaves. These leaves are mostly entire, but include one leaf that is completely lobed (fig. 6). The average height of these plants is about 5.2 cm with an average leaf spread of 7.7 cm (table 1). A faint, reddish pigmentation is usually visible in the roots and crown of this stage.

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[3]All tables are grouped together in the Appendix, beginning on p. 16.
[4]All figures are grouped together in the Appendix, beginning on p. 27.

Seedling stage 3b.--This stage also has five or more basal leaves of which some are entire; however, it is distinguished by having two to four deeply lobed leaves (fig. 7). Reddish pigmentation is usually present in the root and crown. The average height is about 5.6 cm, and the average leaf spread is about 10.8 cm (table 1).

Rosette stage.--This stage has been established as commencing when plants possess at least eight basal leaves of which at least five are completely lobed. The leaves appear to arise together from a short stem and are arranged in a radiating cluster on or near the ground. This stage is further divided into an early and late phase. The early phase has from 8 to 15 leaves, whereas the late phase may have 16 to 26 leaves or more. The average height of a rosette (both phases represented) is about 6.8 cm, and the average diameter (maximum spread) is about 11.9 cm (table 1). A 15-leaf early phase rosette is shown in figure 8.

Vegetative stage (bolting).--This important phenophase is characterized by a full complement of radiating, deeply lobed, basal leaves that are beginning to turn up, and which may have a visible erect stem. When an erect ascending stem is visible, no buds or bud formation are present. The vegetative stage is divided into the following three phases: the beginning or initial bolt phase, which has no evident erect stem, but can be recognized because it possesses a centrally located apical meristem or protuberance that feels hard when pressed; the early bolt phase, which has a visible erect stem that ascends from 1 to 15 cm in length; and the late bolt phase, which is recognized by having an erect ascending stem that extends from 16 to 30 cm or more in length. Figure 9 shows an initial bolt phase, and figure 10 shows an early bolt phase.

Floral bud stage (bud formation).--This stage is distinguished by a developing branched inflorescence, which gives rise to the formation of solitary buds at the ends of branches. There are four recognizable phenophases. In bud stage 1, the beginning bud appears as a small, terminal, swollen protuberance enclosed by bud scales with longitudinally appressed yellow-green spines exposed at the apical end. These spines are usually about one-third of the bud's length (fig. 11). In bud stage 2, the bud becomes ovate in shape and covered with involucral bracts having small medial spines with lateral spinules. The length of the longitudinally appressed yellow-green spines are at this time equal to about one to two times the length of the bud (fig. 12). Bud stage 3 buds appear more globose-ovoid. At this time, the long stout spines have started to rotate, usually not more than 90°, away from the longitudinal axis, but some spines remain clustered along this axis. These long, stout spines are two to three times the length of the bud (fig. 13). Bud stage 4 is characterized by being ovate but larger than the preceding stage. The long stout spines are now straw colored and have rotated completely away from the longitudinal axis, none remaining along this axis (fig. 14).

Anthesis (flowering).--The commencement of flowering is marked by the presence of yellow at the apical opening of the flower head. There are two distinct phenophases during anthesis. Flowering stage 1 is recognized by the appearance of the yellow florets that extend from the apex of the flower head. The florets are tightly appressed and parallel to the longitudinal axis of the flower head (fig. 15). Flowering stage 2 is recognized by the bright yellow ligulate (tongue shaped) florets that are spread out and away from the flower head axis. The yellow area of the spreading florets is equal to or greater than the green involucral bracts that bear the long yellow spines (fig. 16).

Seed formation stage.--This stage can be identified by the loss of the yellow pigmentation in the exposed florets that extend from the apex of the flower head. These florets appear straw colored like the stiff, terete, divergent spines. The involucral bracts still retain chlorophyll at this time (fig. 17).

Mature stage.--At this time, the involucral bracts are devoid of chlorophyll, dry, and tan. The straw-colored florets that distinguished the previous stage are now absent. The seeds have matured, and the light-colored pappus-bearing seeds are ready for dissemination (fig. 18).

Seed dissemination stage.--The flower head appears dry and very much the same as in the mature stage, but with these differences: The involucral bracts have now diverged, and the apex of the flower head has opened; the pappus-bearing achenes have become detached from the receptacle and are now free and suspended in the open bowl of the flower head; and dissemination is usually accomplished by a combination of mechanical agitation and wind movement (fig. 19).

Senescence stage.--This is the final phenophase in the field phenology of yellow starthistle. In this stage, the pappus-bearing achenes have been expelled from the flower head, but the nonpappus-bearing achenes remain intact around the perimeter of the receptacle. The involucral bracts are fully expanded and reveal the empty bowl of the dry, expended flower head. The leaves and stems are commencing to lose their chlorophyll (fig. 20).

Identification of Phenophases

A field key to the different phenophases of *Centaurea solstitialis* is provided below. Each phenophase is characterized by specific differences that are used to separate phenophases. The key should enable a worker to examine a plant and determine the phenophase(s) present.

I. Plants possessing basal leaves only, which may or may not be lobed.

A. Plants with 2, 3, or 4 leaves, no pigmentation in roots (opaque).
Plants with 2 leaves only. *Cotyledon stage 1a*.
Plants with more than 2 leaves, range 3 to 4 leaves. *Seedling stage 1b*.

B. Plants with 5 or more leaves, pigmentation in roots usually reddish, leaves either entire or only partly lobed basally.
Plants with basal leaves entire. *Seedling stage 2a*.
Plants with 1 or 2 basal leaves lobed only in part. *Seedling stage 2b*.

C. Plants with 5 or more leaves, reddish pigmentation in roots and crown; usually, 1 or more deeply lobed leaves.
Plants with basal leaves mostly entire, but include 1 completely lobed leaf. *Seedling stage 3a*.
Plants with basal leaves mostly entire, but include 2 to 4 deeply lobed leaves. *Seedling stage 3b*.

D. Plants with at least 8 leaves, of which at least 5 are completely lobed, arranged in a cluster of radiating leaves appearing to rise from the ground.
Plants with from 8 to 15 leaves. *Early rosette phase*.

Plants with from 16 to 26 or more leaves. *Late rosette phase*.

II. Plants possessing radiating, deeply lobed basal leaves that are beginning to turn up, and which may have an erect stem(s), but without visible buds.

   A. Plants with no evident erect stem, but possessing a centrally protruding, apical, meristem that feels hard when pressed. *Initial bolt phase*.
   B. Plants with evident erect stem(s) from 1 to 15 cm long. *Early bolt phase*.
   C. Plants with evident erect stem(s) from 16 to 30 cm or more long. *Late bolt phase*.

III. Plants with deeply lobed basal leaves and stiff erect stem(s) that may be single or branched and bearing apical buds.

   A. Terminus of stems bears small, swollen protuberance with exposed yellow-green spines at apical end. *Bud stage 1*.
   B. Ovate-shaped bud with extending longitudinally appressed yellow-green spines; spines 1 to 2 times length of bud head. *Bud stage 2*.
   C. Ovate-shaped bud with long (2 to 3 times length of bud head) yellow-green spines; spines radiating away from the longitudinal axis with some spines remaining clustered at or near axis. *Bud stage 3*.
   D. Ovate-shaped bud with stout, yellow spines; all spines have radiated away from the longitudinal axis of the bud. *Bud stage 4*.

IV. Plants possessing both basal and upper leaves with erect branched stems bearing solitary, spined, yellow flower heads at their ends.

   A. Yellow appressed florets visible from apex of the flower head. *Flowering stage 1*.
   B. Yellow florets not appressed but spread out; florets bright yellow, conspicuous. *Flowering stage 2*.

V. Plants possessing both basal and upper leaves with erect branched stems bearing solitary, spined flower heads without bright yellow color.

   A. Florets present, lack bright-yellow pigmentation, straw colored, appear dry. *Seed formation stage*.
   B. Florets absent from flower head; involucral bracts closed at apex, devoid of chlorophyll. *Mature stage*.
   C. Florets absent from flower head; involucral bracts open at apex; pappus-bearing achenes visible and loose in the flower head. *Seed dissemination stage*.
   D. Involucral bracts fully open, flower head conspicuously empty of seeds. *Senescence stage*.

Phenophase Chronology and Weather at Study Sites

Phenophase Chronology

The average percentage of the population represented by each growth stage for each month at each of the three compared sites was recorded over a 3-year

period (tables 2, 3, 4). A population profile of each phenophase and its chronology is graphically portrayed for each of the compared sites. An examination of these results shows that the phenology of the plants in the Hopland population precedes both the Concord and Woodland populations by 2 months; however, all populations senesce at the same time. Also, although a large number of seedlings germinate, intraspecific competition is sufficiently severe to induce a high mortality in this phenophase (figs. 21, 22, 23).

Weather

The influence of abiotic parameters, such as weather, on the seasonal development of yellow starthistle was determined to be different at valley, coastal, and intercoastal sites. The presence of cool temperatures during winter with subsequent summer drought limits the growing season. These alternating climatic conditions apparently result from the influx of cold marine air from polar regions borne eastward with the stormy westerlies, thus producing a characteristically wet winter. During summer, descending air from the subtropical high does not precipitate its moisture and produces a summer drought (Barbour and Major *1977*). The resulting Mediterranean climate, humid winter/arid summer, is therefore typical.

Both zonal circulation and topography are important factors in controlling California's climates (Trewartha *1961*, Patton *1956*). During 1976 and 1977, the severe lack of precipitation produced drought conditions in all of California's floristic provinces. In 1976, the Woodland site (valley) showed the greatest change of the three compared sites, the total precipitation being 179.2 mm versus 255.9 mm at Concord (intercoastal) and 334.4 mm at Hopland (coastal). The annual average temperatures were 16.4°C, 15.8°, and 13.9°, respectively (table 5).

In 1977, the highest total precipitation occurred at Hopland (660.7 mm), followed by Woodland (347.8 mm), then Concord (330 mm). Annual average temperatures were highest at Woodland (16.3°C), followed by Concord (16.1°), then Hopland (14.3°). Both average monthly and annual temperatures and precipitation are given in table 6.

The total precipitation recorded at the compared sites during 1978 was again greatest at Hopland (1020.6 mm), less at Woodland (628.4 mm), and least at Concord (203.2 mm). Average annual temperatures were the same at both Woodland and Concord (16.6°C), but slightly cooler at Hopland (14.4°). Average monthly and annual temperatures as well as average monthly precipitation for 1978 are shown for all sites in table 7.

A comparison of 2-year average temperatures and precipitation at the three study sites for the period coinciding with yellow starthistle seasonal development showed the following: Temperatures at Woodland averaged 3.6°C more than at Hopland and 1.6° more than at Concord. Concord's average temperatures were 2° greater than at Hopland. There were sizable differences in precipitation, Hopland receiving an average 31.9 mm more than Woodland and 49 mm more than Concord. These differences are given in table 8.

Soil samples were taken at all sites from March through September 1976, a drought year, and the percentage of moisture in these samples was determined following the methods described before. As expected, Hopland averaged 8.4 percent soil moisture for these months, whereas Concord averaged 6.9 percent and Woodland, 3.3 percent. The results of these soil moisture determinations are given in table 9 and tend to reflect the precipitation data for these sites during that period.

Population Density

The density of yellow starthistle populations pretty much coincides with precipitation and temperature cycles and the phenophase present at that time. For example, seedlings reach greater densities than any other phenophase, especially when rains favor germination. As summer temperatures increase, population numbers are reduced because of increasing mortality. Differences among the compared study sites largely reflect the differences in precipitation and temperature. The relationships among the indices used to examine population changes were as follows: In general, when density (plants per square meter) increased, the average distance between plants, as well as the average area in square centimeters per plant, decreased, thus an inverse relationship; however, this does not occur in all cases.

Hopland

During 1976, the greatest density occurred during November (589.3 plants per square meter), and the annual average was 130.7 plants per square meter. The annual average distance between plants was 11.6 cm, and the annual average area was 145.5 cm^2 per plant. The monthly data for these indices are given in table 10.

In 1977, abundant precipitation occurred, and yellow starthistle density rose to 615.8 plants per square meter during October. The annual average density was 381.6 plants per square meter (2.9 times greater than the density in 1976) with an annual average distance between plants of as little as 5.3 cm and an annual average area of 29.1 cm^2 per plant. Population fluctuations for 1977 are given in table 10.

In 1978, high density (212.5 plants per square meter) occurred in January. The annual averages were: density, 150.7 plants per square meter; distance between plants being 8.4 cm and average area per plant being 72.6 cm^2. Monthly variations in these indices are given in table 10.

Concord

During 1976, a high density of only 17 plants per square meter was recorded for this site in March, the annual averages being: 7 plants per square meter; 43.8 cm^2 between plants; and 2039.3 cm^2 mean area per plant. Table 11 shows monthly changes in these indices.

The high density for 1977 was 9.4 plants per square meter, which occurred in March, with an annual average of 6.1 plants per square meter. Plants were very sparse, average distance between plants being 42 cm and average area per plant being 1808.1 cm^2. Monthly densities are given in table 11.

The Concord populations reached a high density of 22.1 plants per square meter during March of 1978, with an annual average of 12.4 plants per square meter. Average distance between plants was 30 cm, and average area was 930.7 cm^2 per plant. Monthly changes in the population are given in table 11.

Woodland

In 1976, the high point of the population occurred in March, a density of 315.5 plants per square meter being recorded; these were all seedlings. The annual averages were 101.3 plants per square meter; average distance between plants was 24.9 cm; and average area, 905.5 cm^2 per plant. Monthly changes are given in table 12.

The 1977 density was highest during February at 238.9 plants per square meter, the annual average being 91.5. Distance between plants averaged 21.7 cm, and the area per plant averaged 691.5 cm^2 for the year. Monthly fluctuations are given in table 12.

The highest recorded density in 1978 was 18.6 plants per square meter, which occurred in February. The population declined greatly, the annual averages being: 8.8 plants per square meter; average distance between plants, 38.8 cm; and average area, 1606.1 cm^2 per plant. The recorded monthly fluctuations are given in table 12.

A comparison of the average total density over the 3-year period (1976-78) at each site showed the following: Hopland averaged 221; Concord, 8.4; and Woodland, 67.2 plants per square meter. Also, plants at the Concord site had the greatest distance between them (38.6 cm) and the greatest area per plant (1592.7 cm^2).

Seed Germination Data, 1977

The number of seeds germinating and producing young plants that were counted and removed monthly from the established five areas (900 cm^2 per area) at each site, during the time that germination occurred, were as follows:

At Hopland, from February to June 1977, 1,153 seedlings ($\bar{x}$ = 288.3) germinated from the sampled seed reservoir. The ratio of seedlings germinating per area squared varied from one plant:5 cm^2 in February to one plant:562.5 cm^2 in May (table 13).

A total of 617 seedlings ($\bar{x}$ = 154.3) germinated in the sampled areas at Woodland during the same period. The ratio of seedlings germinating per area squared ranged from one plant:7.8 cm^2 in February to one plant:562.5 cm^2 in May (table 13).

Seedlings germinating in the sample areas at Concord did not commence until March and were complete by May. A total of 134 seedlings ($\bar{x}$ = 67) germinated. During the brief germination period, the ratio of seedlings per area squared ranged from one plant:34.6 cm^2 in March to one plant:1125 cm^2 in April (table 13).

A comparison of the three study sites showed that seed germination at Hopland was 1.9 times greater than at Woodland and 4.3 times greater than at Concord, and Woodland was 2.3 times greater than at Concord.

Physical Measurements of Mature Plants

Measurements of 25 mature plants from each site in September 1976 showed that the average height of the Hopland population was 78.5 cm, the Woodland population was 63.1 cm, and the Concord population was 45.3. The average width of the Woodland plants, however, was greater ($\bar{x}$ = 62.8 cm) than either the Hopland group (40.2 cm) or the Concord group ($\bar{x}$ = 29.1 cm). The average height, width, and standard deviation of these populations are given in table 14.

Seed Production and Kinds of Seeds

Seed production in yellow starthistle is comprised of two kinds of seeds as described previously. A comparison of seed production at the three study sites, using several indices, is reported herein. Plants sampled in the Woodland population produced an average of 267.3 seed heads per plant as compared with 25.5 at Hopland and 19.3 at Concord (table 15). This constituted 10.5 times as many seed heads as Hopland and 13.9 times as many as Concord plants. The average number of seeds per seed head was 43.1 at Concord, 38.1 at Hopland, and 37.5 at Woodland. The calculated seed production per plant (average number of seed heads times average number of seeds per head) is 10,023.7 seeds for Woodland, 831.8 for Concord, and 716.5 for Hopland. The Woodland plants were prolific, producing 14 times as many seeds per plant as Hopland and 12 times as many as Concord.

A comparative examination of the average number of pappus-bearing seeds per seed head from the different populations studied was as follows: The average number of pappus-bearing seeds was 35.5 at Concord, 34.1 at Hopland, and 28.9 at Woodland (table 16). The ratio of pappus-bearing to nonpappus-bearing seeds was 4.7:1 at Concord, 8.7:1 at Hopland, and 3.4:1 at Woodland.

DISCUSSION

A comparison of the three yellow starthistle populations shows some similarities and some differences. The growth stages and substages are the same and are recognizable in all populations; however, the chronology and other indices of the Hopland population differ from that of both Woodland and Concord. Important among these differences are abiotic parameters such as precipitation (Hopland, 44 percent greater than Woodland; 68 percent greater than Concord), annual average temperature (Woodland, 1.6°C greater than Concord; 3.6° greater than Hopland), and the percent of moisture in soil (Hopland, about 2 percent more than Concord; 5 percent more than Woodland). Other indices that differ include: a greater average population density, earlier phenology, and greater average plant height at Hopland than at Woodland or Concord. There are also differences in the total seed production per plant as well as the ratio of pappus-bearing to nonpappus-bearing seeds. Because the phenology of the Hopland population is initiated earlier (October versus December for Woodland and Concord), this suggests the importance of the coastal weather pattern on Hopland plants. The considerably greater precipitation (1.8 times greater than Woodland; 3.1 times

greater than Concord) that occurs seasonally at Hopland, for the period coinciding with the growth cycle of yellow starthistle, has quite likely been a major parameter in causing natural selection for plants that have the capability for early response, as has been recorded for the Hopland population.

Although the phenophases are completed at the same time (September and October) for all three populations under field conditions, the cooler average temperatures recorded for Hopland, versus higher average temperatures at Woodland and Concord, are probably responsible for slowing down the Hopland plants, hence, completion of the field phenology at the same time in all three populations. However, plants grown from seeds from all three populations, when grown under standard conditions of soil, water, and temperature, demonstrated that plants from the Hopland population complete their phenology in significantly less time than do plants from the Woodland and Concord populations (D. M. Maddox and N. A. Stevens, unpublished data).

Also of interest are the differences in seed production and different ratios of the two kinds of seeds present in these populations. The pappus-bearing seeds are extruded at maturity and serve to perpetuate the species during more optimum conditions, whereas the nonpappus-bearing seeds are persistent and function to perpetuate the species during adverse times or conditions. Roche (*1965*) showed that the nonpappus-bearing seeds have a higher temperature requirement for germination and produce a seedling with a significantly greater rate of radicle elongation than do those of pappus-bearing seeds. Furthermore, he concluded that "these characteristics are of survival value related to seasonal fluctuations of temperature and moisture." Since the results of this study show that the Woodland and Concord populations grow under more adverse conditions of precipitation and temperature than those at Hopland, one might expect to find different plant survival strategies invoked in these plant populations. An examination of these results tends to support this assumption. The ratio of pappus-bearing to nonpappus-bearing seeds is greatest in the Hopland population (8.7:1), less at Concord (4.7:1), and least at Woodland (3.4:1).

In conclusion, the likely evolution of the yellow starthistle in California, as indicated by the data presented here, suggests that the California plants are probably represented by different allopatric populations that are responding (by genotypic differentiation) to the environmental differences prevailing in different habitats. Turesson (*1922*, *1925*) interpreted such a genotypic response of a plant species to habitat differences as being a basic constituent in the origin of adaptive races in plants.

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APPENDIX

Tables

Table 1.--*The average height, spread, and standard deviation of yellow starthistle stages except vegatative and floral bud stages*

Sample No.	Growth stage	Average height	± SD	Maximum spread	± SD
		Cm		*Cm*	
20	Cotyledon 1a	0.95	0.22	1.52	0.50
20	Seedling 1b	1.08	.34	1.63	.46
20	Seedling 2a	1.30	.41	3.05	.97
20	Seedling 2b	5.60	2.90	5.85	2.59
20	Seedling 3a	5.18	2.11	7.73	3.12
20	Seedling 3b	5.65	2.22	10.78	2.62
20	Rosette[1]	6.80	2.73	11.90	5.87
25	Mature plant	62.29	16.62	44.03	17.17

[1]Sample contained both early and late-phase rosettes.

Table 2.--*Average percentage of population and chronology of each growth stage at Hopland, Calif., over a 3-year period, 1976-79*

	Growth stages								
Month	Seed-lings	Ro-sette	Vegeta-tive	Floral bud stage	Anthe-sis	Seed forma-tion	Ma-ture	Seed dis-semi-nation	Sene-scence
July			2	55	36	7			
August				4	2	42	12	40	
September							35	32	33
October	89								11
November	100								
December	95	5							
January	89	11							
February	85	15							
March	94	6							
April	85	15							
May	50	9	41						
June	1		52	47					

Table 3.--*Average percentage of population and chronology of each growth stage at Concord, Calif., over a 3-year period, 1976-79*

Month	Growth stages								
	Seed-lings	Ro-sette	Vegeta-tive	Floral bud stage	Anthe-sis	Seed forma-tion	Ma-ture	Seed dis-semi-nation	Sene-scence
July			6	43	15	11		25	
August				3	2	9	14	70	2
September							37	56	7
October								1	99
November									
December	88	12							
January	82	18							
February	75	25							
March	82	18							
April	62	38							
May	37	15	47	1					
June	4	3	47	45	1				

Table 4.--*Average percentage of population and chronology of each growth stage at Woodland, Calif., over a 3-year period, 1976-79*

Month	Growth stages								
	Seed-lings	Ro-sette	Vegeta-tive	Floral bud stage	Anthe-sis	Seed forma-tion	Ma-ture	Seed dis-semi-nation	Sene-scence
July	2		35	43	11	3		6	
August				4	4	11	17	60	4
September				2			14	73	11
October								19	81
November									
December	100								
January	100								
February	98	2							
March	94	6							
April	92	8							
May	62	7	3	28					
June	3	3	67	26	1				

Table 5.--*Average temperatures and total precipitation at study sites during 1976*

[Dashed line indicates initiation of yellow starthistle growth cycle]

Month	Woodland		Hopland		Concord	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
	°C	*Mm*	*°C*	*Mm*	*°C*	*Mm*
January	7.6	10.7	6.1	11.4	9.1	66.0
February	10.4	20.6	8.4	69.3	11.1	36.1
March	12.1	39.4	9.0	44.2	12.4	43.7
April	14.2	29.0	10.4	77.5	14.1	4.8
May	20.9		16.3		18.8	
June	22.9	3.1	19.1		20.8	
July	25.3		22.5	.5	21.3	
August	22.6	10.9	19.9	37.8	21.2	12.4
September	22.4	15.5	20.2	3.3	20.7	21.3
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October	18.4	9.4	16.6	11.2	18.5	14.2
November	12.8	17.5	12.4	63.7	13.4	17.0
December	7.4	23.1	5.4	15.5	8.7	40.4
Annual average.	16.4	14.9	13.9	27.9	15.8	21.3
Total precipitation.		179.2		334.4		255.9

Table 6.--*Average temperatures and total precipitation at study sites during 1977*

[Dashed line indicates initiation of yellow starthistle growth cycle]

Month	Woodland		Hopland		Concord	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
	°C	*Mm*	*°C*	*Mm*	*°C*	*Mm*
January	5.8	40.4	6.3	58.7	7.3	36.8
February	10.9	27.2	10.4	67.3	11.9	35.6
March	11.2	52.1	8.4	76.2	4.5	42.7

Table 6.--*Average temperatures and total precipitation at study sites during 1977*--Continued

[Dashed line indicates initiation of yellow starthistle growth cycle]

Month	Woodland		Hopland		Concord	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
	°C	*Mm*	*°C*	*Mm*	*°C*	*Mm*
April	17.4	1.0	13.6	3.8	16.4	7.6
May	16.0	36.3	12.2	54.4	12.1	10.7
June	24.3		21.1		28.2	
July	24.6		22.5		23.9	
August	24.4		23.1	.8	23.3	
September	21.4	12.7	19.2	54.6	21.1	14.5

October	18.2	11.2	15.6	33.8	19.2	3.3
November	12.1	78.5	10.4	103.6	14.2	71.9
December	9.4	88.4	8.4	207.5	11.7	106.9
Annual average.	16.3	29.0	14.3	55.1	16.1	27.5
Total precipitation.		347.8		660.7		330.0

Table 7.--*Average temperatures and total precipitation at study sites during 1978*

[Dashed line indicates initiation of yellow starthistle growth cycle]

Month	Woodland		Hopland		Concord	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
	°C	*Mm*	*°C*	*Mm*	*°C*	*Mm*
January	9.8	278.9	8.9	431.0	11.6	11.4
February	10.4	111.3	9.7	206.8	12.4	39.1
March	14.5	116.3	12.6	132.8	15.1	29.5
April	14.4	45.0	11.1	141.7	14.6	57.4
May	21.1	1.0	16.1	5.6	19.3	2.3

Table 7.--*Average temperatures and total precipitation at study sites during 1978*--Continued

[Dashed line indicates initiation of yellow starthistle growth cycle]

Month	Woodland		Hopland		Concord	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
	°C	*Mm*	*°C*	*Mm*	*°C*	*Mm*
June	22.9		19.2	.8	20.9	
July	24.9		22.8		22.7	
August	25.1		23.0	.5	23.1	
September	22.4	9.1	18.9	54.1	21.3	7.6
October	19.4		17.9		19.6	
November	9.9	66.8	8.7	30.5	12.0	38.1
December	4.9		4.3	16.8	6.2	17.8
Annual average.	16.6	52.4	14.4	85.1	16.6	16.9
Total precipitation.		628.4		1,020.6		203.2

Table 8.--*A comparison of 2-year average temperatures and precipitation at the study sites for the period coinciding with yellow starthistle seasonal development*

Time period	Woodland		Hopland		Concord	
	Average temperature	Average precipitation	Average temperature	Average precipitation	Average temperature	Average precipitation
	°C	*Mm*	*°C*	*Mm*	*°C*	*Mm*
10/76-10/77	16.2	18.3	14.3	33.9	15.8	18.3
10/77-10/78	19.9	61.6	14.7	109.9	17.2	27.5
2-year average.	18.1	40.0	14.5	71.9	16.5	22.9

Table 9.--*Average percentage of moisture in soil during months of March through September 1976 at study sites*

Month samples taken	Average moisture in soil at study sites		
	Hopland	Concord	Woodland
	Percent		
March	12.3	18.3	6.9
April	16.5	9.2	4.5
May	8.8	5.5	2.7
June	5.2	4.7	---
July	3.4	3.8	1.2
August	---	2.7	---
September	4.1	4.1	1.4
Average	8.4	6.9	3.3

Table 10.--*Population density of yellow starthistle at Hopland during annual growth cycle, 1976-78*

[Dashed line indicates initiation of yellow starthistle growth cycle]

Year and month	Average distance between plants	Average area	Total density
1976	*Cm*	*Cm^2/plant*	*Plants/m^2*
March	13.4	178.8	55.9
April	12.3	151.0	66.2
May	11.0	120.3	83.1
June	10.5	109.8	91.1
July	12.0	143.8	69.6
August	14.2	202.8	49.3
September	15.5	240.9	41.5
Growth cycle average.	12.7	163.9	65.2
November	4.1	17.0	589.3
1977			
January	4.6	20.8	481.0

Table 10.--*Population density of yellow starthistle at Hopland during annual growth cycle, 1976-78*--Continued

[Dashed line indicates initiation of yellow starthistle growth cycle]

Year and month	Average distance between plants	Average area	Total density
1977 (Continued)	*Cm*	*Cm*^{2}*/plant*	*Plants/m*^{2}
February	4.9	24.5	408.2
March	4.7	21.6	462.5
April	5.2	26.8	372.7
May	4.9	24.1	414.8
June	5.4	28.7	348.1
July	6.0	36.1	276.9
August	6.5	41.6	240.4
September	7.2	51.1	195.6
Growth cycle average.	5.3	29.2	378.9
October	4.0	16.2	615.8
1978			
January	6.9	47.1	212.5
February	7.1	49.7	201.2
April	7.1	50.4	198.4
May	8.2	67.1	149.0
June	8.7	75.8	132.0
July	9.8	95.6	104.6
August	9.3	87.0	114.9
September	10.4	107.8	92.8
Growth cycle average.	7.9	66.3	202.4

Table 11.--*Population density of yellow starthistle at Concord during annual growth cycle, 1976-78*

[Dashed line indicates initiation of yellow starthistle growth cycle]

Year and month	Average distance between plants	Average area	Total density
1976	*Cm*	*Cm*^{2}*/plant*	*Plants/m*^{2}
March	24.3	588.5	17.0
April	31.4	987.8	10.1
May	41.1	1687.6	5.9

Table 11.--*Population density of yellow starthistle at Concord during annual growth cycle, 1976-78*--Continued

[Dashed line indicates initiation of yellow starthistle growth cycle]

Year and month	Average distance between plants	Average area	Total density
1976 (Continued)	*Cm*	*Cm^2/plant*	*Plants/m^2*
June	55.9	3125.9	3.2
July	44.0	1936.0	5.2
August	59.4	3531.9	2.8
September	46.7	2185.6	4.6
Growth cycle average.	43.3	2006.2	7.0
December	47.7	2271.5	4.4
1977			
January	37.6	1413.0	7.1
February	37.6	1411.5	7.1
March	32.6	1065.4	9.4
April	34.6	1194.4	8.4
May	39.4	1550.0	6.5
June	39.4	1555.5	6.5
July	48.6	2361.0	4.2
August	50.1	2514.0	4.0
September	48.7	2369.7	4.2
Growth cycle average.	41.6	1770.6	6.2
October	51.4	2646.1	3.8
1978			
February	22.7	514.4	19.4
March	21.3	451.6	22.1
May	29.8	890.7	11.2
June	33.5	1119.4	8.9
July	33.8	1145.0	8.7
August	34.4	1183.9	8.5
September	34.8	1209.7	8.3
Growth cycle average.	32.7	1145.1	11.4

Table 12.--*Population density of yellow starthistle at Woodland during annual growth cycle, 1976-78*

[Dashed line indicates initiation of yellow starthistle growth cycle]

Year and month	Average distance between plants	Average area	Total density
1976	*Cm*	*Cm^2/plant*	*Plants/m^2*
March	5.6	31.7	315.5
April	7.2	52.0	192.4
May	20.0	401.6	24.9
June	28.1	791.3	12.6
July	36.1	1299.6	7.7
August	44.8	2007.9	5.0
September	51.2	2619.4	3.8
Growth cycle average.	27.6	1029.1	80.3
December	6.3	40.2	248.8
1977			
January	10.2	104.2	95.9
February	6.5	41.9	238.9
March	7.1	50.5	197.8
April	8.3	69.6	143.8
May	7.3	53.1	188.2
June	20.7	429.3	23.3
July	33.1	1094.3	9.1
August	42.2	1781.7	5.6
September	40.9	1670.4	6.0
Growth cycle average.	18.3	533.5	115.7
October	40.3	1620.1	6.2
1978			
February	23.2	537.3	18.6
March	24.1	588.2	17.5
May	37.7	1424.9	7.0
June	45.8	2097.4	4.8
July	46.0	2118.1	4.7
August	48.0	2301.1	4.3
September	46.7	2180.9	4.6
Growth cycle average.	39.0	1608.5	8.5

Table 13.--*Germination of seed in soil in 5 30-cm² areas per site in 1977*

Month	Hopland ratio		Woodland ratio		Concord ratio	
	Seedlings	Seedlings per area squared	Seedlings	Seedlings per area squared	Seedlings	Seedlings per area squared
	Number	*Cm²*	*Number*	*Cm²*	*Number*	*Cm²*
February	895	1: 5	574	1: 7.8	0	
March	182	1: 24.7	33	1: 136.4	130	1: 34.6
April	68	1: 66.2	2	1:2250	4	1:1125
May	8	1:562.5	8	1: 562.5	0	
June	0		0		0	
Total	1,153		617		134	
Average	288.3		154.3		67	

Table 14.--*Height and width of mature plants measured at study sites in September 1976*

Indices	Study sites		
	Hopland	Woodland	Concord
Plant number measured	25	25	25
Average maximum height (cm)	78.5	63.1	45.3
SD of maximum height (cm)	12.1	11.7	16.1
Average maximum width (cm)	40.2	62.8	29.1
SD of maximum width (cm)	12.6	14.4	32.8

Table 15.--*Number of seed heads per plant at the study sites*

Study site	Plants	Seed heads	Average seed heads per plant	SD
	Number			
Hopland	52	1,324	25.5	19.1
Concord	10	193	19.3	13.9
Woodland	10	2,673	267.3	188.9

Table 16.--*Number of seeds per seed head and number of pappus- and nonpappus-bearing seeds in yellow starthistle at study sites*

Indices	Study sites		
	Hopland	Concord	Woodland
Number of seed heads	28	27	10
Total number of seeds	1,066	1,164	375
Average number of seeds/seed head	38.1	43.1	37.5
Total number of pappus-bearing seeds.	956	958	289
Average number of pappus-bearing seeds/seed head.	34.1	35.5	28.9
SD of pappus-bearing seeds	8.15	15.43	9.85
Total number of nonpappus-bearing seeds.	110	206	86
Average number of nonpappus-bearing seeds/seed head.	3.9	7.6	8.6
SD of nonpappus-bearing seeds	2.32	4.01	6.02

Figure 1.--Cotyledon stage 1 a.

Figure 2.--Seedling stage 1 b (3-leaf).

Figure 3.--Seedling stage 1 b (4-leaf).

Figure 4.--Seedling stage 2 a.

Figure 5.--Seedling stage 2 b.

Figure 6.--Seedling stage 3 a.

Figure 7.--Seedling stage 3 b.

Figure 8.--Rosette stage (15 leaves).

Figure 9.--Vegetative stage (beginning bolt).

Figure 10.--Vegetative stage (early bolt).

Figure 11.--Floral bud stage Bu-1.

Figure 12.--Floral bud stage Bu-2.

Figure 13.--Floral bud stage Bu-3.

Figure 14.--Floral bud stage Bu-4.

Figure 15.--Anthesis stage F-1.

Figure 16.--Anthesis stage F-2.

Figure 17.--Seed formation stage.

Figure 18.--Mature stage.

Figure 19.--Seed dissemination stage.

Figure 20.--Senescence stage.

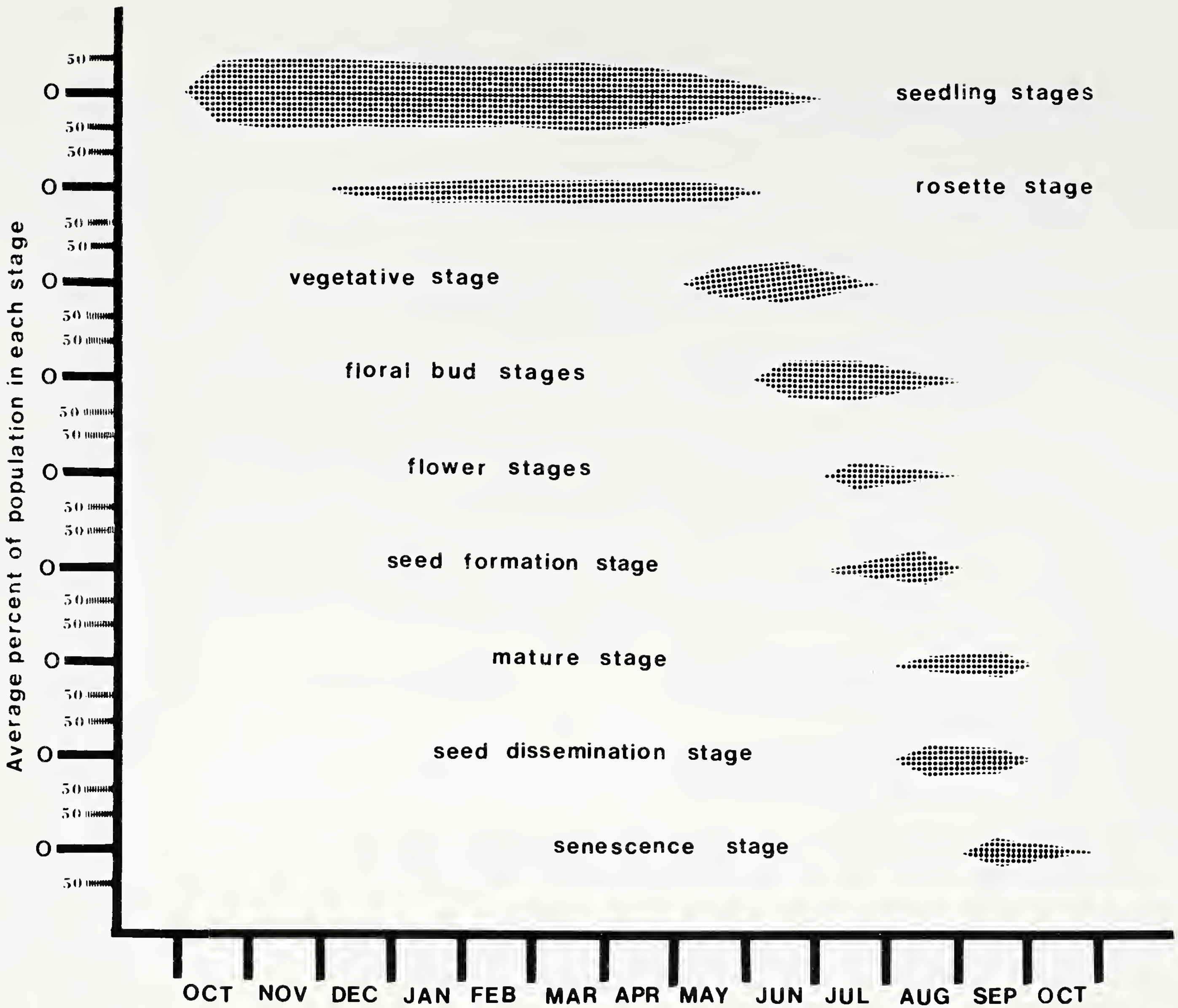

Figure 21.--Seasonal development of yellow starthistle at Hopland, Calif., during a 3-year period.

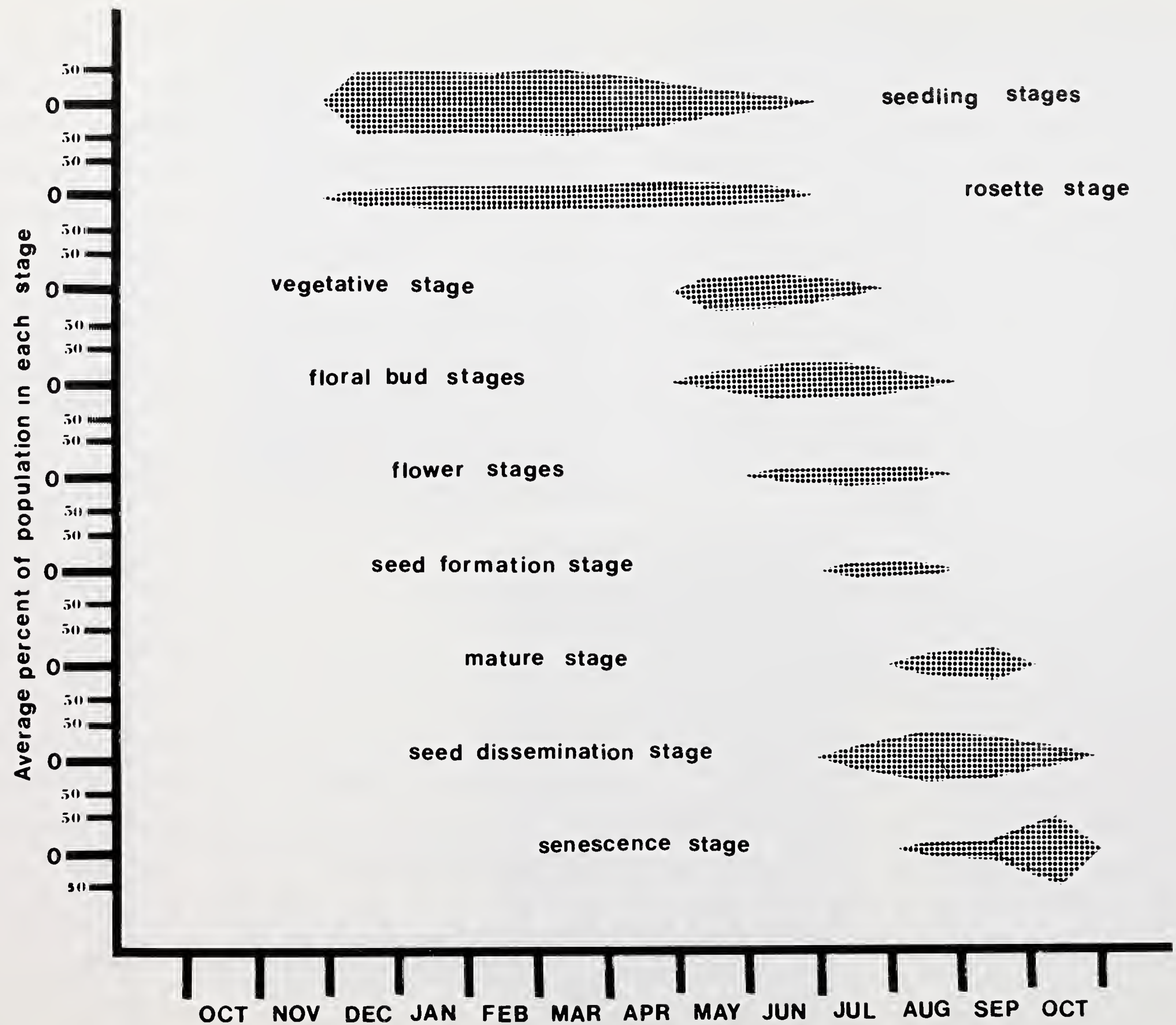

Figure 22.--Seasonal development of yellow starthistle at Concord, Calif., during a 3-year period.

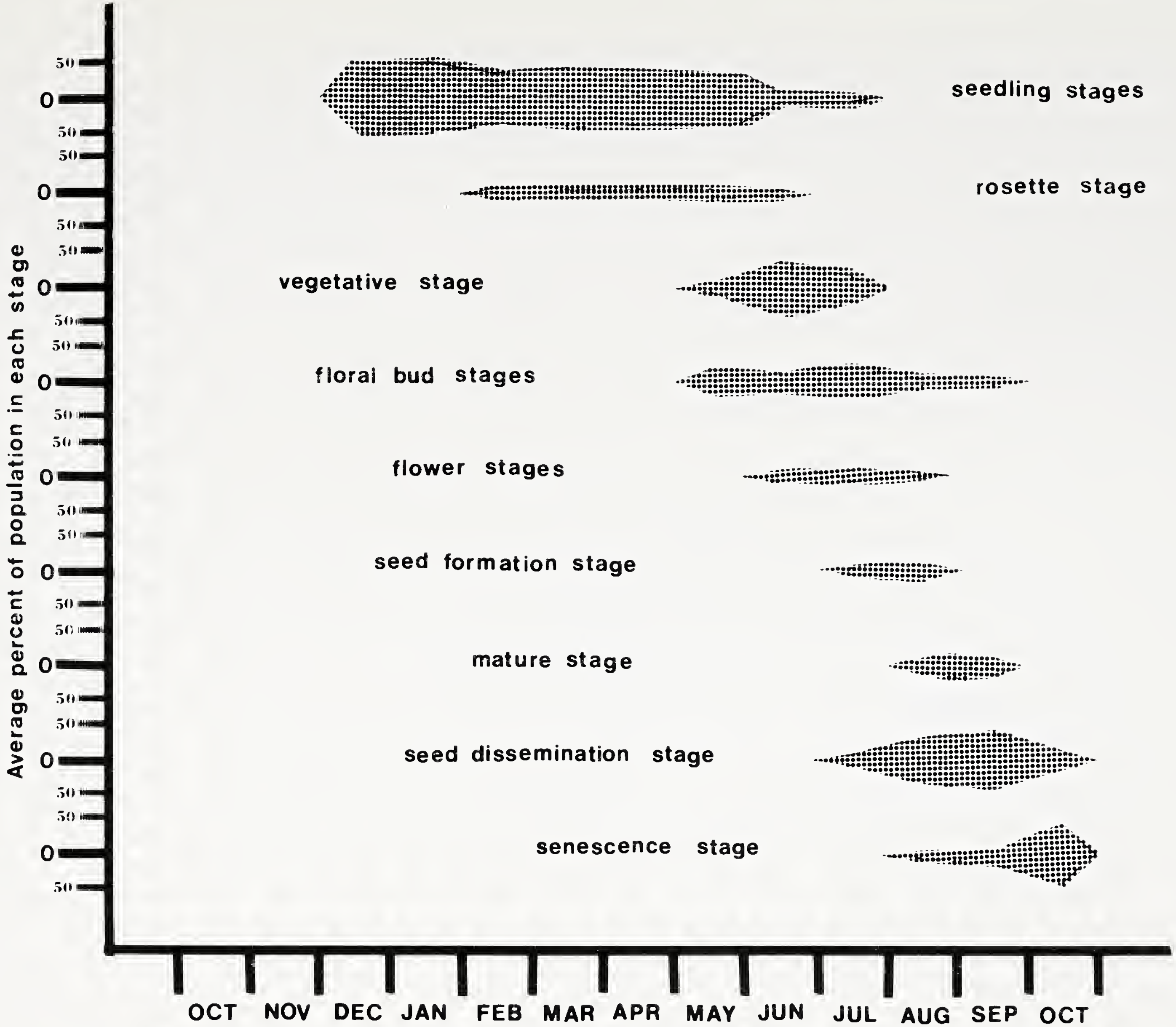

Figure 23.--Seasonal development of yellow starthistle at Woodland, Calif., during a 3-year period.

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